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Relative Occurrence of the Family Kalotermitidae (Isoptera) under Different Termite Sampling Methods

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Abstract

The termite family Kalotermitidae constitutes a wood-nesting termite family that accounts for about 15% of all extant termite species. In recent decades, field studies have been carried out to assess termite diversity in various wooded habitats and geographic locations. Three sampling methods have been favored expert, transect, and alate light-trap surveys. Expert collecting is not spatially quantifiable but relies on field personnel to recognize and sample termite niches. The transect method aims to standardize and quantify termite abundance and diversity. Light trapping is a passive method for sampling nocturnal alate flights. We compared our expert survey results and results of published sampling methods for their proportional yields of kalotermitid versus non-kalotermitid encounters. Using an odds ratio statistic, we found that worldwide, there is about a 50.6-fold greater likelihood of encountering a kalotermitid sample versus a non-kalotermitid using the expert survey method and a 15.3-fold greater likelihood using alate trapping than using the transect method. There is about a 3.3 -fold greater likelihood of collecting a kalotermitid specimen versus a non-kalotermitid sample using the expert survey method than using the alate trap method. Transect studies in which only termite species diversity was reported gave similar low Kalotermitidae yields. We propose that multiple biases in sampling methodology include tools, time constraints, habitat type, geographical location, topographical conditions, and human traits account for the divergent outcomes in sampling the abundance and diversity of Kalotermitidae compared to other termite families.

Introduction

Social insects are dominant inhabitants of tropical landscapes (Wilson and Hölldobler, 2005), and assessing their ecological significance requires astute taxonomic knowledge. Species identifications rely on keys and descriptions of known and new taxa that are often obtained by deliberate collecting expeditions. Field surveys to assess the known and unknown diversity and abundance of social Hymenoptera and termites require different collecting methods. Because of their open foraging behavior, most ants are collected with baits, trapping by pitfall or Malaise devices, or passively sifting litter with Winkler bags (Agosti & Alonso 2000, Ellison et al., 2007, Longino et al., 2002). Similarly, social wasps are most commonly collected in baited traps and Malaise traps (De Souza & Prezoto, 2006, Noll & Gomes, 2009, Rezende Diniz & Kitayama, 1998, Silveira, 2002). Eusocial bees can be attracted with fragrances or caught in trap nests (Feja, 2006). Active collecting by hand or net is also used for ants, bees, and wasps.

Because of their cryptic nature, termites cannot be collected passively with traps or baits but must be acquired directly from within the substrata they inhabit. This requires digging, chopping, scraping, or probing into soil, wood, nest material, and foraging tubes to expose and collect termites. As discussed later, imagoes that disperse at night can be collected with light traps and, on occasion, open-foraging termites have been collected in pitfall traps (Willis et al., 1992) or attracted to scattered baits such as instant oatmeal flakes (Scheffrahn & Rust, 1983). Long-term cellulose baiting has been used to attract some termites as well (Dawes-Gromadzki, 2003, Davies et al., 2013).

In recent years, a series of termite sampling studies was published with the stated goal of defining species abundance and diversity of termites at a given locality. To accomplish this, the transect protocol of Jones and Eggleton (2000), or slightly modified versions thereof, were developed from the protocols first set forth in the 1990s to examine the contribution of soil fertility by soil-inhabiting termites (Anderson & Ingram, 1993). More recent publications continue to address termite sampling protocols, but again, from a "soil" perspective (Bignell, 2009, Moreira et al., 2008). Therefore, the emphasis on sampling soil-inhabiting termites was a intended priority in transect surveys. For example, a compilation of 87 transects from 29 tropical locations (Davies et al., 2003b) revealed that only 13 out of 1511 termite occurrences (0.86%) consisted of non-soil inhabiting termites (i.e., Kalotermitidae).

The termite family Kalotermitidae is composed of nearly 500 extant species worldwide (Krishna et al., 2013a). The Kalotermitidae are broadly distributed and their diversity is the greatest near the equator. With one exception, all studied kalotermitids nest in galleries excavated within single pieces of sound or partially decayed wood. The dimensions of their host wood can range from mere twigs to massive boles with the majority of field-collected kalotermitids taken from dead tree limbs. Unlike the kalotermitids, species of the other two major termite families (Rhinotermitidae and Termitidae, ca. 2,400 spp.) forage beyond their nest boundaries; either below the soil surface, under earthen or fecal tubing, or on open substrata.

Results of termite diversity surveys using alate traps have yielded very different taxonomic compositions compared to transect methods. This indicates that kalotermitids are underrepresented in transect surveys. Of the five studies employing light traps (all neotropical: Bourguignon et al., 2009, Gomes da Silva Medeiros et al., 1999, Martius, 2003, Martius et al., 1996, Robello & Martius, 1994) 11.4% of the imagoes collected were kalotermitids. A tree canopy transect in Panama (Roisin et al., 2006) yielded an even higher proportion (34.9%) of kalotermitids.

From 1990 to 2014, we conducted termite survey expeditions in the New World with the goal of collecting as much diversity ("species richness") over the largest area and most varied habitats and microhabitats as time and cost permitted (e.g., Scheffrahn et al., 2003, 2005, 2006). Our "expert" surveys and those in Taiwan by Li, H. F, et al. (2011, 2015) also yielded higher proportions (2.6-61.5%) of kalotermitid colony occurrences (unique encounters) than those of transect studies from comparable habitats.

In this paper, we review termite sampling methods and compare them for their proportional yields of kalotermitid versus non-kalotermitid encounters. We offer some hypotheses to explain the disparate ratios of encounters between these two distinct termite groups.

Materials and Methods

Expert Survey

Our expert collecting method was devised (Scheffrahn et al., 1990) to maximize termite taxon diversity while minimizing collecting time at a given site. The primary goal of expert collecting was to build and enrich the holdings of the University of Florida Termite Collection (UFTC) in Davie, Florida. The FLREC currently housed 43,426 unique colony samples. When planning termite surveys, site locations were not determined in advance of expeditions, although general travel routes were selected to include as many habitats and biomes that could be sampled in the time allotted. Most site selections were dictated by daylight visibility, motor vehicle travel routes, vehicle parking (roads with shoulders or turnoffs), and human accessibility (steep slopes or flooded areas were avoided). Habitats of little human disturbance were preferred but often not available. Barbed wire fences, drainage ditches, and noxious roadside vegetation were often traversed to access collectable areas. Sites above arm's reach were seldom sampled. Each site was surveyed from about five to 90 minutes by groups (one to nine team members) of experienced collectors. Each collector was free to choose his or her own search strategy at each site. If a species at a given locality was found to be very common, it was likely that multiple samples of that species were collected, however, it was also communicated among the team members to stop collecting abundant species, e.g. *Nasutitermes corniger*, and focus on other termites. It was also unlikely that multiple samples were collected from the same colony because disturbance or damage denoted that the spot had already been collected by a team member. If multiple samples were collected from a single colony, e.g. a large log containing kalotermitids, the vials are bound by rubber bands to denote a single sample. Sites generally covered 0.1 to about 50 hectares and yielded from zero to over 60 colony samples. In most cases, travel time between sites was approximately equal to time spent collecting termites.

The primary tool for each collector was a 32-cm-long, 0.9 kg hatchet. The hatchet was used to open sound to rotten branches, logs, stumps, fence posts, nest carton, epigeal mounds, etc. The hatchets were also used to dig into soil or to pry or lift objects lying on the soil surface such as logs, stones, dung pats, etc. A Teflon®-lined cooking pan was used to hold extracted termites and associated debris. An aspirator was used to suction termites from debris for photography and transfer into 2-dram glass vials (Fisher Scientific no. cat. No. 03-339-26B) filled with 85% ethanol After each expedition, samples were cleaned by removing soil and other fine debris and adding more 85% ethanol. A unique inventory code label was added to each vial for curation and long-term storage in the UFTC. All collection sites were georeferenced either from paper maps (before 1997) or GPS receiver coordinates. Site elevations were confirmed using Google™ Earth. Samples are stored in an air-conditioned room inside closed storage cabinets. Using this curation method, many UFTC samples > 20 years-old have yielded full 654 bp barcode (CO1) DNA sequences.

In recent years, only two other taxon-quantified expert surveys have been published outside the New World. Li et al. (2011) used axes and aspirators to sample termite diversity in a Taiwanese pangolin habitat. Li, H. F, et al. (2015) collected termites within 100 m diam plots in a tropical forest ecosystem in Taiwan. Collecting tools were not specified. Expert collecting has occasionally been called "casual collecting" as in the case of Gathorne-Hardy & Jones, 2000.

Transect Surveys and Alate Trapping

The transect protocol of Jones & Eggleton (2000) was developed as a standardized termite sampling protocol; "to measure termite species richness and functional diversity in tropical forests." [Of note: In response to Roisin and Leponce (2004), Jones et al. (2006) gave a conflicting goal for their transect protocol: ….."measuring species density and relative abundance is for us more illuminating than estimating species richness."]. Regardless, the method of Jones and Eggleton (2000) specifies that transects be divided into 5x2 m sections and each section sampled for one hour "in the following microhabitats….samples of surface soil (each about 12x12 cm, to 10 cm depth); accumulations of litter and humus at the base of trees and between buttress roots; *the inside of dead logs, tree stumps, branches and twigs*; the soil within and beneath very rotten logs; all subterranean nests, mounds, carton sheeting and runways on vegetation, and arboreal nests up to a height of 2 m aboveground level" (italics emphasize typical kalotermitid microhabitats). All transect studies listed in Table 1 cite either the method of Jones and Eggleton (2000) or specify a modification thereof, but all mention sampling from potential kalotermitid microhabitats. A single canopy transect, conducted by Roisin et al. (2006), employed professional tree climbers who cut dead branches from trees and inspected standing stock greater than 10 m above ground. The cut limbs were then searched for termites.

Table 1. Studies listing occurrences of kalotermitid and non-kalotermitid termites in wooded habitats by sampling method.

Region or Biome	Sampling Method	No. Kalo Occurrences	No. Non-Kalo Occurrences	Total Termite Occurrences	% Kalo of Total Occurrences	Reference
Subtropical & Tropical New World						
New World	Expert survey	10368	20208	30576	33.9	current study
Central America	Expert survey	795	4044	4839	16.4	current study
Ecuador, Amazonia	Expert survey	28	1035	1063	2.6	current study
NW mainland	Expert survey	3058	15623	18681	16.4	current study
Panama	Expert survey	138	1373	1511	9.1	current study
Peru, Amazonia	Expert survey	31	952	983	3.2	current study
South America	Expert survey	692	8108	8800	7.9	current study
United States	Expert survey	1270	1066	2336	54.4	current study
West Indies	Expert survey	7310	4585	11895	61.5	current study
Argentina, Chaco	Std. Transect	3	29	32	9.4	Godoy et al., 2012
Argentina, Chaco	Mod. Transect	40	175	215	18.6	Roisin & Leponce, 2004
Brazil, Amazonia, Manaus	Alate Traps	1581	9991	11572	13.7	Martius, 2003
Brazil, Amazonia, Manaus	Alate Traps	1919	23555	25474	7.5	Martius et al., 1996
Brazil, Amazonia, Manaus	Alate Traps	2095	8625	10720	19.5	Robello & Martius, 1994
Brazil, Amazonia, Manaus	Std. Transect**	0	306	306	0.0	Ackerman et al., 2009
Brazil, Amazonia, Manaus	Std. Transect	2	162	164	1.2	Dambros et al., 2013
Brazil, Amazonia, Manaus	Std. Transect	0	692	692	0.0	Dambros et al., 2016a
Brazil, Atlantic forest	Alate Traps	1140	10227	11367	10.0	Gomes da Silva et al., 1999
Brazil, Atlantic forest	Std. Transect	26	701	727	3.6	Cancello et al., 2014
Brazil, Atlantic forest	Std. Transect	11	314	325	3.4	Reis & Cancello, 2007
Brazil, Atlantic forest	Std. Transect	5	189	194	2.6	Vasconcellos et al., 2010
Brazil, Atlantic forest	Std. Transect	2	178	180	1.1	Viana-Junior et al., 2014
Brazil, Atlantic forest	Mod. Transect	20	162	182	11.0	Bandeira et al., 2003
Brazil, Atlantic forest	Mod. Transect	11	406	417	2.6	Couto et al., 2015
Brazil, Atlantic forest	Mod. Transect	8	390	398	2.0	Souza et al., 2012
Brazil, Atlantic forest	Mod. Transect	5	160	165	3.0	Vasconcellos et al., 2005
Brazil, Central Amazonia	Mod. Transect	12	4375	4387	0.3	Dambros et al., 2016b
Brazil, Northeast	Mod. Transect	12	612	624	1.9	Ernesto et al., 2014
Brazil, Northeast	Mod. Transect	1	431	432	0.2	Almeida et al., 2017***
Brazil, Pantanal	Std. Transect	0	53	53	0.0	da Cunha et al., 2015
Brazil, plantation	Mod. Transect	0	160	160	0.0	Calderon & Constantino, 2007

Table 1. Studies listing occurrences of kalotermitid and non-kalotermitid termites in wooded habitats by sampling method. (Continuation)

Region or Biome	Sampling Method	No. Kalo Occurrences	No. Non-Kalo Occurrences	Total Termite Occurrences	% Kalo of Total Occurrences	Reference
Subtropical & Tropical New World						
Brazil, Presidente Figueiredo	Std. Transect	3	268	271	1.1	Dambros et al., 2012
Brazil, Southeast Cerrado	Std. Transect	0	219	219	0.0	Oliveira et al., 2013
Brazil, Southeast Cerrado	Mod. Transect	0	64	64	0.0	Carrijo et al., 2009
Brazil, Southeast Cerrado	Std. Transect	0	754	754	0.0	Silva et al., 2016
Brazil, Southeast Cerrado	Mod. Transect	7	108	115	6.1	Alves et al., 2011
Colombia, Amazonia	Mod. Transect	0	278	278	0.0	Florian et al., 2017
French Guiana	Std. Transect	6	3184	3190	0.2	Davies et al., 2003a
French Guiana, Amazonia	Mod. Transect	5	851	856	0.6	Bourguignon et al., 2011
Panama	Canopy Transect	22	41	63	34.9	Roisin et al. 2006
Panama	Alate Traps	84	467	551	15.2	Bourguignon et al. 2009
Panama	Mod. Transect	1	242	243	0.4	Roisin et al., 2006
Panama	Mod. Transect	1	143	144	0.7	Basset et al., 2017
Peru, Amazonia	Mod. Transect	0	967	967	0.0	Dahlsjo et al., 2015
Peru, Amazonia*	Std. Transect	1	246	247	0.4	Palin et al., 2011
Tropical Africa						
Benin	Std. Transect	0	443	443	0.0	Hausberger & Korb, 2016
Burundi	Std. Transect	0	1070	1070	0.0	Nduwarugira et al., 2017
Cameroon	Mod. Transect	0	849	849	0.0	Deblauwe et al., 2007
Guinea	Std. Transect	0	473	473	0.0	Dosso et al., 2012
Ivory Coast	Std. Transect	0	626	626	0.0	Dosso et al., 2010
Malawi	Std. Transect	0	190	190	0.0	Donovan et al., 2002
Nigeria	Std. Transect	0	120	120	0.0	Kemabonta & Balogun, 2015
South Africa	Std. Transect, Baits	0	1015	1015	0.0	Davies et al., 2013
Asia						
Asia, Southeast	Std. Transect	15	3509	3524	0.4	Gathorne-Hardy et al., 2002
Borneo	Std. Transect	1	195	196	0.5	Jones et al., 2000
Borneo	Std. Transect	2	439	441	0.5	Jones et al., 2010
Borneo	Std. Transect	2	378	380	0.5	Jones & Prasetyo, 2002
China, Guangdong	Mod. Tansect	0	179	179	0.0	Li, Z.Q., et al., 2015
Indonesia, Krakatau	Std. Transect	11	498	509	2.2	Gathorne-Hardy et al., 2000
Java	Std. Transect	0	88	88	0.0	Pribadi et al., 2011
Malaysia	Std. Transect	0	265	265	0.0	Hanis et al., 2014
Malaysia	Mod. Transect	10	1259	1269	0.8	Eggleton et al., 1999
Sarawak	Std. Transect	0	25	25	0.0	Jamil et al., 2017
Sri Lanka	Std. Transect	1	160	161	0.6	Hemachandra et al., 2010
Sumatra	Std. Transect	3	1178	1181	0.3	Gathorne-Hardy et al., 2001
Sumatra	Std. Transect	1	283	284	0.4	Jones et al., 2003
Taiwan	Expert survey	28	105	133	21.1	Li, H. F., et al., 2011
Taiwan	Expert survey	275	397	672	40.9	Li, H. F., et al., 2015
Thailand	Std. Transect	1	198	199	0.5	Inoue et al., 2006
Vietnam	Mod. Transect	0	154	154	0.0	Duc et al., 2017
Vietnam	Mod. Transect	0	228	228	0.0	Van Quang et al., 2017
Tropical Australia						
E. Australia	Mod. Tansect	0	597	597	0.0	Houston et al., 2015
N. Australia	Mod. Tansect	0	57	57	0.0	Dawes-Gromadzki, 2005
N. Australia	Mod. Tansect	0	80	80	0.0	Dawes-Gromadzki, 2008
Worldwide review						
Old & New World Tropics	Std. Transect	38	2105	2143	1.8	Davies et al., 2003b

*Three Peruvian habitats were surveyed. The Amazonian rainforest yielded 72% of species; none were kalotermitids.
**Jones and Eggleton (2000).
***Kalotermitid misidentified as *Paraneotermes*.

As with many other flying insects, light traps are effective in capturing termite alates but due to greater morphological ambiguity of this caste, most termite collectors seek soldiers and workers. Earlier studies of regional termite diversity (e.g., New World: Banks & Snyder, 1920, Emerson, 1925, Mathews, 1977; Old World: e.g. Sjöstedt, 1925, Emerson, 1928) did not quantify taxon occurrences but reported collections of alates around lights. The first taxon-quantified termite survey from alate trap catches was conducted by Robello & Martius (1994) near Manaus, Brazil. Ultraviolet light traps were placed at 3.6 or 4 m height and sampled for 24 months. Similar techniques were used in subsequent alate trapping studies.

We compiled our expert survey results and summarized literature results from transect, alate trap, and expert studies of wooded habitats with regard to kalotermitid and non-kalotermitid occurrences (Table 1). We also compiled results in which species diversity of kalotermitid and non-kalotermitid termites was reported from transect surveys, but individual occurrences were not enumerated (Table 2).

Statistical Analysis

An odds ratio (OR) statistic was used to measure the effect of collection method on kalotermitid vs. non-kalotermitid encounters of the three main collection methods in Table 1 (canopy transect excluded). Three pairs of comparisons were considered: 1) transect vs. alate traps, 2) transect vs. expert survey, and 3) alate traps vs. expert survey. For each method pair, a 2x2 matrix comparison of percentages was used: 1) number of kalotermitids collected in method 1 (e.g. transect), 2) number of non-kalotermitids collected in method 1 (e.g. transect), number of kalotermitids collected in method 2 (e.g. alate traps), and number of non-kalotermitids collected in method 2 (e.g. alate traps). Odds-ratios were computed for geographic regions where at least two survey methods were applied using two-sided p values for the test of independence with Fisher's exact test.

Table 2. Studies in which occurrences of kalotermitid and non-kalotermitid termites was not enumerated. Wood was sampled in each study.

Region or Biome	Sampling Method	No. Kalo spp.	No. Non-Kalo spp.	% Kalo spp.	Reference
SE Brazil	Mod. Transect	0	14	0.0	Araújo et al., 2007
Panama	Std. Transect	1	16	6.3	Basset et al., 2017
Brazilian Amazonia	Mod. Transect	9	76	11.8	Bandeira, 1989*
Brazilian Amazonia	Mod. Transect	0	78	0.0	Constantino, 1992
NE Brazil	Mod. Transect	5	45	11.1	Couto et al., 2015
Thailand	Std. Transect	0	16	0.0	Davies, 1997
French Guiana	Std. Transect	4	96	4.2	Davies, 2002
Cameroon	Std. Transect	0	88	0.0	Eggleton et al., 1995
Borneo	Std. Transect	3	63	4.8	Eggleton et al., 1997
Tropical West Africa	Std. Transect	1	132	0.8	Eggleton et al., 2002a
Congo	Std. Transect	0	80	0.0	Eggleton et al., 2002b
Benin	Std. Transect	0	20	0.0	Hausberger et al., 2011
Cameroon	Std. Transect	0	117	0.0	Deblauwe et al., 2007
Cameroon	Std. Transect	0	47	0.0	Jones & Eggleton, 2000
Sabah Malaysia	Std. Transect	0	33	0.0	Jones & Eggleton, 2000
Peninsular Malaysia	Std. Transect	0	29	0.0	Jones & Eggleton, 2000
Sumatra, Indonesia	Std. Transect	1	54	1.9	Jones et al., 2003
Vietnam	Std. Transect	0	43	0.0	Neoh et al., 2015
Sumatra, Indonesia	Std. Transect	0	21	0.0	Neoh et al., 2016
SE Brazil	Std. Transect	1	49	2.0	Nunes et al., 2017
Thailand	Mod. Transect	0	35	0.0	Sornnuwat et al., 2003

* Occurrence of Incisitermes is dubious.

Results

Table 3 gives the ORs ($p < 0.001$) for each pairing of survey methods by geographic region (Table 1). Worldwide, there is about a 50.6-fold greater likelihood using the expert survey method and a 15.3-fold greater likelihood using alate trapping of encountering a kalotermitid sample versus a non-kalotermitid than using the transect method. There is about a 3.3 -fold greater likelihood of collecting a kalotermitid versus a non-kalotermitid using the expert survey method than with the alate trap method. For the New World, the results show about a 10-fold higher likelihood of collecting a kalotermitid versus a non-kalotermitid using the alate traps method than with the transect method, a 33.8 times higher chance of collecting a kalotermitid versus and non-kalotermitid using the expert survey than with the transect method, and a 3.3 times higher chance of collecting of collecting a kalotermitid versus a non-kalotermitid using the expert survey method than with the alate trap method. For Asia, the results show about 115.7 times higher odds of collecting a kalotermitid (and not a non-kalotermitid) with the expert survey than with the transect method. Of the 20 transect studies in which species were recorded but the number of individual occurrences were not enumerated, 13 failed to detect any kalotermitids, and seven reported the composition of kalotermitid species between 0.8 and 11.8% (Table 2).

Table 3. Odds ratios (OR) and their 95% confidence intervals (CI) between different survey methods for encountering a kalotermitid sample. All Odds ratios in the table are significantly different from 1.0 (p<0.001).

Survey methods		World total	Subtropical & Tropical New World	Tropical Asia
Expert survey vs. transect	OR	50.5	33.8	115.7
	CI	(44.6, 57.6)	(29.4, 39.0)	(83.7, 162.7)
Expert survey vs. alate traps	OR	3.3	3.2	N/A
	CI	(3.2, 3.4)	(3.2, 3.4)	
Alate traps vs. transect	OR	15.5	10.4	N/A
	CI	(13.7, 17.7)	(9.0, 12.0)	

Discussion

The first notable taxonomic treatises based on expert field surveys of termites were conducted around the start of the previous century (e.g., Haviland, 1898, Sjöstedt, 1900, Silvestri, 1903, Holmgren, 1906) all of which recorded many new kalotermitids. With the assistance of expert collectors, Nathan Banks described 12 new kalotermitid species between 1901 and 1920 (data from Krishna et al., 2013a). The "Emerson Era" (Krishna et al., 2013b) began with Emerson's (1925) expert survey of Guyana where he collected 12 kalotermitid species, 11 of which were new. Expert collections by Emerson, Light, Krishna, Snyder and their collaborators added an additional 100 new extant kalotermitid species between 1918 and 1962 (data from Krishna et al., 2013a). Since, 1962, approximately 170 new kalotermitid species have been described as a result of expert collections. Using the expert survey method, we attempted to maximize termite taxon diversity while minimizing collecting time. In addition to finding many novel termitids, we have collected and described 22 new kalotermitid species and expanded the range of many more taxa. At least 20 more new kalotermitids are pending description from our expert surveys. As far as we know, only one new kalotermitid species, *Cryptotermes chacoensis* Roisin, has been collected and described from transect survey material (Roisin & Leponce, 2004).

The stated goal of the transect protocol is to assess both termite species richness (diversity) and functional group (feeding niche) in tropical forests (Jones & Eggleton, 2000). Our finding of kalotermitid underrepresentation in transect surveys when compared to other methods is likely rooted in multiple sampling biases. These might include collecting tools, time constraints, habitat type, geographical location, topographical conditions, and human traits (experience, search patterns, collecting skills, hiking ability, eyesight, etc.). Alate traps may offer the most unbiased estimate of local termite composition, albeit for crepuscular or nocturnal fliers. Because different species have different flight seasons, traps must be tended over long periods; time-costly and difficult to accomplish in remote sites. The five alate trap surveys given in Table 1 yielded between 7.5 and 19.5% kalotermitid occurrences. The actual ratio of kalotermitid-to-nonkalotermitid colonies is probably greater than absolute occurrence because kalotermitid colonies have lower populations than their nonkalotermitid counterparts.

Central to the performance of field surveys are the tools used and how selected tools affect collecting time and efficiency. For termites, two types of collecting tools are required; tools to access the termites and tools to handle and transfer the termites into ethanol. For access, a hoe is more efficient in excavating soil than an ax, but a hoe is not designed to split and open wood. Curiously, the types of tools to use for standard transect surveys have never been specified although they are likely variants of a hoe as used by Reginaldo Constantino or Tiago Carrijo (Scheffrahn pers. obs.). Darlington (1992, 1997) used a cutlass (machete) to split wood. Emerson (1938) mentions the use of a hatchet for opening nests during his collecting expedition in Guyana (Emerson, 1925). Li et al. (2011) used axes. Roisin et al. 2006 "cut down" tree branches using saws free from time constraints of ground-based transects. It is interesting to note that Bandeira (1989), who collected the highest proportion of kalotermitid species (11.8%, Table 2), used a chain saw to systematically sample dead wood.

For handling and transfer, forceps can be used (e.g., Ackerman et al., 2007) which excludes the transfer of termites from their niche detritus, but forceps require more field time than an aspirator. Aspiration also collects large groups of termites before they can escape with little or no specimen damage. Aspirated samples are rinsed of detritus in the laboratory allowing more field collecting time.

Kalotermitids require more time to collect than non-kalotermitid species. The transect protocol allocates 30 min sampling time by two trained people per 5x2 m plot (Jones & Eggleton, 2000). But even with an ax, splitting wood is strenuous and consumes time in the search for morphologically identifiable castes in the galleries of sound wood. Whereas excavating rotten wood, nests, or the surface soil is less strenuous and may not require an ax. Expert surveys accommodate sampling for kalotermitids because they employ the tools for splitting wood, are not confined to a defined search area (but within walking distance), and are not limited to a specific search time. Comparisons of termite diversity yields between transect and expert collecting methods is problematic because field sampling is biased by human traits (experience, collecting skills, hiking ability, physical condition, etc.) and the physical environment. Jones & Eggleton, 2000 stated that their field assistants were sufficiently trained to conduct transect sampling after one practice transect but suggested that their performance could be affected by motivation. Other unquantifiable human qualities affecting collection efficiency include recognition of termite microhabitats, willingness to enter thick and/or spiny undergrowth or standing water, strength, and work performance in uncomfortable weather. Motivation to discover novel taxa for our expert surveys is driven by a competitive spirit and peer pressure.

But what is the difference in cost of an expert collecting expedition versus a transect survey? To get a rough idea, we compare our 2012 country-wide expert survey of Paraguay with our 2011 on-foot expert survey of Parque Nacional Yasuní, Ecuador. The Ecuador expedition is a reasonable proxy for a transect survey because it was conducted at a single locality. The cost of vehicle rental, fuel expense, and tolls for Paraguay (2,075 km driven by two vehicles) amounted to about $3,500 USD, an expense not needed for Yasuní. The collecting time lost to driving was substantial, however, travel allowed for sampling fauna in Paraguay's highly varied biomes. The non-monetary "cost" of traveling great distances on unfamiliar foreign roads is the inherent danger of a traffic accident. The Paraguay expedition yielded 1,288 colony samples (54 kalotermitid samples) with a 60 person-day collecting effort. Yasuní yielded 1,035 samples (28 kalotermitids) with a 45 person-day effort.

For species richness, probably the most comparable of the two sampling methods is the Jones & Eggleton (2000) single transect in Mbalmayo Forest Reserve, Cameroon (+3.45°, +11.47°), and our first full day of expert collecting at Yasuní (-0.674°, -76.398°). Both are tropical rain forests, but probably with greater overall termite diversity at Mbalmayo. Jones and Eggleton (2000) yielded 47 species (no kalotermitids) after four person-days of sampling. We collected 59 species (8 kalotermitid samples) after 7.5 person-days, suggesting rather similar diversity yields, excepting for the Kalotermitidae. But does the transect method really reflect the local fauna, specifically the Kalotermitidae? Jones & Eggleton (2000) concluded that "The taxonomic and functional group composition of the transect samples did not differ significantly from that of the known local fauna." We offer limited evidence that in similar biomes, at least for Kalotermitidae, that these may differ. Table 4 compares the kalotermitid and nonkalotermitid samples collected in the Peruvian Amazon from Palin et al. 2011, Dahlsjö et al., 2015, and data from our unpublished 2014 survey. The former two transect studies yielded a single unidentified kalotermitid, collected at 1500 m, from a combined total of 1,214 nonkalotermitid samples collected from 190 m to 1500 m. Our survey yielded 31 kalotermitids from six different genera from a total of 983 samples.

Geographical attributes, habitat types, and topographical conditions also bias kalotermitid encounters. Our experience in the Neotropics suggests that oceanic islands (e.g. West Indies) offer the greatest abundance and relative diversity of kalotermitids followed by littoral mainland localities (e.g., Panama) with inland forests showing the least in abundance and diversity (e.g., Amazonian Peru). For example, our expert survey results revealed that the island of Jamaica has 10 endemic kalotermitid species compared to 4 non-kalotermitids, while Panama yielded 23 kalotermitids compared to 53 nonkalotermitids, and the Peruvian Amazon produced only 12 kalotermitid species compared to 95 non-kalotermitids (Scheffrahn et al. unpublished). Because of their overwater dispersal abilities (Yamane et al., 1992, Scheffrahn & Postle, 2013), islands become filters for Kalotermitidae. Littoral zones support tree species that are tolerant to tidal exposure and sandy soil. The low kalotermitid abundance in inland rain forests may be an artifact of the inability to assess high tree branches (Roisin et al., 2006). It is likely that transect plots are set on relatively flat surfaces while expert sampling allows for collecting along steep trails and hillsides, roadsides, and narrow shorelines.

While it is impossible to collect all termite species in a particular locality, all survey methods contribute to the discovery of new species and termite diversity in a given area. Herein we show that the expert colleting method should be preferred for collecting greater diversity and abundance of the Kalotermitidae.

Table 4. Kalotermitid versus nonkalotermitid sampling yields from three Peruvian Amazon termite surveys.

	Palin et al. 2011			Dahlsjö et al. 2015	current study		
Method		Std. transect		Mod. transect		Expert	
Elevation (m)	190	925	1500	190	≤190	204 - 1104	≥1500
Latitude (°)	-12.83	-12.95	-13.05	-12.82	-8.60 to -8.37	-11.29 to -8.49	-10.72 to -10.71
Longitude (°)	-69.28	-71.53	-71.54	-69.27	-74.94 to -74.72	-76.04 to -74.67	-75.18 to -75.14
Kalo./nonkalo.	0/189	0/55	1/3	0/967	5/153	25/810	1/20
Kalo. genera	-	-	unknown	-	*Calcaritermes* *Glyptotermes* *Neotermes*	*Calcaritermes* *Comatermes* *Cryptotermes* *Glyptotermes* *Rugitermes*	*Rugitermes*

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